

THE OHIO JOURNAL OF SCIENCE

PUBLISHED BY THE
OHIO STATE UNIVERSITY SCIENTIFIC SOCIETY

VOLUME XVIII

APRIL, 1918

No. 6

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THE PARASITES OF LEAF-HOPPERS.

With Special Reference to the Biology of the Anteoninæ.

F. A. FENTON.

PART I.

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INTRODUCTION.

The study of the parasites of the leaf-hoppers presents an interesting problem, not only from the practical standpoint, but from the biological as well. The economic status of the leaf-hoppers has been well established, and as a group they are now considered as including some of the more important insect pests. Therefore, their control by parasitism is significant as a natural check, and their parasites must be considered as dis-

tinctly beneficial. This fact has been utilized in actual practice in control measures against the sugar-cane leaf-hoppers in Hawaii with marked success.

From the biological viewpoint, the study of the interrelations of these parasites with their host has a direct bearing upon the interesting problem of insect parasitism in general. Thus the specialization of the dryinid, and the morphological changes it brings about in its host, the hopper, may and probably does have parallels in the relations between other groups of parasitic insects with their hosts.

These Homoptera are subject to parasitism in all their stages; namely, egg, nymphal, and adult. In North America three orders of insects are known to contribute their quota of the parasites of this group—the *Hymenoptera*, *Diptera*, and *Strepsiptera*; and in Australia and Hawaii, certain of the *Lepidoptera* are considered to be parasitic, though this relation is not definitely established.

The eggs are known to be parasitized by species of the *Platygastridæ*, *Mymaridæ*, *Encyrtidæ*, *Eulophidæ*, and *Trichogrammidæ* (Perkins, 1905-1906). The nymphs and adults are parasitized by the *Anteoninæ*, *Pipunculidæ*, *Strepsiptera*, *Epipyropidæ* and *Encyrtidæ* (Perkins, 1905) and *Chalcididæ* (Misra, 1917).

The relative importance of these parasites as natural checks varies probably in different localities. However, in Ohio, at least in the northern half, the *Anteoninæ* are the most important. *Strepsiptera* have been recorded as being relatively numerous in regions further south, and their rather obscure habits and small size possibly may account for an underestimation of their importance in this locality. Frequently their host survives and thus it seems that their attack is not always fatal. Certainly, however, they form an important link in the chain of natural enemies.

The following paper is confined to an account of the *Anteoninæ*. Material was more plentifully obtained for their study, and their greater importance warranted a more extended investigation. Most of the parasites used in the life history studies were bred from hoppers taken near Sandusky and Columbus, Ohio.

ACKNOWLEDGMENTS.

The writer is greatly indebted to Professor Herbert Osborn, at whose suggestion the work was started, for his continued aid throughout the entire study. He also wishes to thank Mr. D. M. DeLong for the collection and identification of parasitized *Cicadellidæ* from Tennessee, Mr. F. H. Lathrop for the collection of material from Oregon, and Mr. S. H. Rohwer, of the U. S. National Museum, for the use of type material in the identification of species.

HISTORICAL.

Latreille (1805) described *Lestodryinus* (*Dryinus*) *formicarius* which is the earliest record of description of a representative of this group. Jurine (1807) described a species which now forms the type of the genus *Anteon*. Ljungh (1810) described *Gonatopus formicarius* as the first apterous form and Dalman (1818) described *Aphelopus melaleucus*. Each of these species are typical of the four tribes into which the *Anteoninae* are now divided.

The first host record was by Curtis in 1836, when he reported *Aphrodes craticula* to be parasitized in different stages by these parasites. Edward Perris in 1857 thought that *Platygonatopus* (*Gonatopus*) *pedestris* (Dalm.) was a hyperparasite of *Euscelis Athysanus maritimus*, believing that the larval sac was the primary parasite and distinct from the dryinid. G. von Frauenfeld (1865) mentioned *Platygonatopus* (*Gonatopus*) *pedestris* (Dalm.) in connection with (*Typhlocyba*). Since *Erythroneura* (*Typhlocyba*) is parasitized only by the genus *Aphelopus* in this family, it is probable that the host record is incorrect.

Lichtenstein (1874) reported rearing a species, *Gonatopus ptinorum* from the beetle *Ptinus fur* but Kieffer (1914) considers this species as *Cephalonomia xambeni* Giard of the sub-family *Bethylinæ*. From 15 to 20 larvæ were found in the cocoon of *Ptinus*, each spinning up an individual cocoon after issuing from the host (Kieffer '14). Dale (1878) mistook a probable dryinid larva for an Acarid and named it *Homopterophagus dorsettensis*. It was reared from a black, "mustard seed-like structure, noticed on the sides of diverse *Homoptera*, near the insertion place of the wings." According to Kirkaldy this was the larva of *Gonatopus*.

Mik (1882) described and worked out several important stages in the life history of *Gonatopus pilosus* Thoms. showing the true nature of the parasite to the host and disproving the hyperparasite theory. Giard (1889) noticed and described the dryinid sacs attached to *Erythroneura hypocastani* in France and remarked upon the sac-like structure believing it to be a "true animal gall produced on an arthropod by another arthropod." In a later article in this same year he succeeded in rearing the adult parasite which proved to be *Aphelopus melaleucus* Dalm. He noticed the similarity of his own observations with regard to the hosts and life history with those of Perris (1857) and Mik (1882) and concluded that as a group the *Anteoninae* were generally parasitic on the (*Jassidae*) *Cicadelidæ*. Giard also noticed certain secondary sexual modifications on the host caused by the parasite and that the hoppers were castrated.

Swezey (1903) reared both sexes of two dryinids from leaf-hoppers and these were identified by Ashmead. He was thus the first one to associate the males of the more highly specialized apterous females and his true interpretation of the so-called genus *Labeo* in connection with these marks an important step in the knowledge of these insects.

Perkins (1905) gave a detailed account of the biology and life history of the *Anteoninae*, together with descriptions of a large number of genera and species new to science, he having further divided the old genus *Gonatopus* into a number of distinct genera based on more exact structures than the general body form. He also gave an extended host list and the next year supplemented this with new additions from Arizona.

Kieffer (1907) summarized the knowledge of the group to that year in a work that was primarily systematic and later (1914) monographed the group under the *Bethylidæ*. Perkins (1912) in reviewing Kieffer's first paper added a number of new species, publishing four excellent plates figuring a number of typical *Anteoninae*.

Keilin and Thompson (1915) worked out some very important points in the biology of *Aphelopus melaleucus* Dalm., especially with regard to the very early stages and the production and development of the peculiar hypertrophied tissue in the host. In December of this same year and in 1916 Kornhauser worked out the biology of *Aphelopus theliæ*

Gahan, Mss. giving the first authentic record of a dryinid being parasitic on a membracid and also being the first one to observe polyembryony in this group. His work is concerned primarily with the effects of parasitism on the host.

Misra (1917) in working upon the Indian sugarcane leaf-hopper, *Pyrilla aberrans* Kirby, gave a number of pages to the discussion of the biology of the two dryinid parasites of this group.

SYSTEMATIC POSITION.

The *Anteoninae* (*Dryinidae*) are now generally considered to be a sub-family of the *Bethylidae*, the latter being included in the super-family *Proctotrupoidea* of the Hymenoptera. A further discussion of the systematic relationships of these insects will be taken up in Part II of this paper.

METHODS.

All the parasites mentioned in the life history studies of this paper were bred, it being very difficult to capture adults in the field. All the hoppers were kept alive and the parasitized ones isolated in separate shell vials provided with a layer of damp soil and a cotton plug. Fresh leaves were added every day until the host had been killed by the parasite. When the latter had issued the host shell was preserved dry in gelatine capsules. If the hopper died before the parasite matured, it was preserved in 70 per cent. alcohol. The material for the morphological studies was sectioned, or dissected in cedar oil, being transferred into the latter directly from 70 per cent. alcohol.

DISTRIBUTION.

Geological.—Kieffer reports the genera *Dryinus* and *Chelognus* from the lower Oligocene and Brues a new genus *Dryininae* from this same stratum.

Geographical.—The *Anteoninae* are found in all parts of the world and will doubtless be found wherever their hosts are abundant. According to Kieffer up to 1914 there have been 396 certain species described and 28 doubtful species. Of these, 200 have been described from the Palearctic region, 98 from the Nearctic, 65 Australian, 32 Neotropical, 16 Oriental, and 8 so far from the Ethiopian regions. To the list of countries Alaska may be added, one species of *Deltocephalus* being quite

extensively parasitized. It is probable that they are cosmopolitan in their distribution as a group.

Host Records.—As previously stated, the *Anteoninae* confine their attacks to the *Fulgoridae*, *Cicadellidae* and *Membracidae* so far as is known at the present, with but one record in the last named family.*

The following list summarizes the host records in so far as have been ascertained to date. The names and systematic position of the hosts have been arranged chiefly after Van Duzee's latest catalogue, (1917).

HOST LIST.

MEMBRACIÆ.

Host Species	Stage of Host	Parasite Species	Authority	Location
<i>Thelia bimaculata</i>	nymphs	<i>Aphelopus theliæ</i>	Kornhauser	Evanston, Ill.

CICADELLIDÆ.

Sub-family *Bythoscopinæ*.

<i>Agallia sanguinolenta</i>	5th instar	?	F. A. F.	Marietta, Ohio. H. O.
<i>Ipo</i> sp.	nymph and adult	<i>Parenteon myrmecophilus</i>	Perkins	Queensland, Australia.
<i>Eurinoscopus</i> sp.	nymph	<i>Chelogynus leiosomus</i>	Perkins	Queensland, Australia.
<i>Eurinoscopus</i> sp.	nymph	<i>Chelogynus nitidus</i>	Perkins	Queensland, Australia.
<i>Eurinoscopus</i> sp.	nymph	<i>Chelogynus dinudiatus</i>	Perkins	Queensland, Australia.
<i>Eurinoscopus</i> sp.	nymph and adult	<i>Chelogynus destructor</i>	Perkins	Queensland, Australia.
<i>Idiocerus</i> sp.	nymph	<i>Chelogynus cognatus</i>	Perkins	Queensland, Australia.
<i>Idiocerus pallidus</i>	nymph and adult	?	F. A. F.	Corvallis, Oregon F. H. L.
? <i>Macropsis</i>	nymph	<i>Chelogynus cognatus</i>	Perkins	Queensland, Australia.

*Ratzeburg reported rearing *Aphelopus albipes* (Ratzeb.) from pupæ of *Bombyx pudibunda*, and Surface, *Phorbas longicornis* (Brues) from the cocoon of a microlepidopteron. Both of these records are doubtful and in the latter case it is probable that the cocoon of the dryinid itself was mistaken for the lepidopterous cocoon.

Sub-family *Jassinæ*.

Host Species	Stage of Host	Parasite Species	Authority	Location
<i>Parabolocratus flavidus</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Scaphoideus immistus</i>	Adult and nymph	?	F. A. F.	Venice, Ohio.
<i>Tartessus syrtides</i>	?	<i>Chalcogonatopus gigas</i>	Perkins	Queensland, Australia.
<i>Euleimomos</i> sp.	adult	<i>Chelognus parvulus</i>	Perkins	Queensland, Australia.
<i>Euleimomos</i> sp.	adult	<i>Chelognus coriaccus</i>	Perkins	Queensland, Australia.
<i>Euleimomos</i> sp.	adult	<i>Pachygonatopus melanicus</i>	Perkins	Queensland, Australia.
<i>Euleimomos</i> sp.	?	<i>Gonatopus vitiensis</i>	Perkins	Fiji.
<i>Platymetopius pyrops</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Platymetopius acutus</i>	nymph	?	F. A. F.	Columbus, Ohio.
<i>Phrynophyes</i> sp.	?	<i>Chalcogonatopus decoratus</i>	Perkins	Queensland, Australia.
<i>Deltocephalus</i> sp.?	nymph and adult	<i>Digonatopus australiæ</i>	Perkins	Queensland, Australia.
<i>Deltocephalus</i> sp.?	?	<i>Gonatopus dubiosus</i>	Perkins	Queensland, Australia.
<i>Deltocephalus</i> sp.?	nymph	<i>Chelognus pallidicornis</i>	Perkins	Queensland, Australia.
<i>Deltocephalus</i> sp.?	nymph	<i>Chalcogonatopus optabilis</i>	Perkins	Queensland, Australia.
<i>Deltocephalus</i> sp.?	?	<i>Gonatopus ombrodes</i>	Perkins	Columbus, Ohio.
<i>Deltocephalus</i> sp.?	nymph	<i>Gonatopus vitiensis</i>	Perkins	Queensland, Australia.
<i>Deltocephalus sayi</i>	adult	<i>Gonatopus contortulus</i>	F. A. F.	Castalia, Ohio.
<i>Deltocephalus sayi</i>	adult	<i>Gonatopus</i> n. sp.	F. A. F.	Columbus, Ohio.
<i>Deltocephalus sayi</i>	nymph	?	F. A. F.	Columbus, Ohio.

Sub-family *Jassina*—Continued.

Host Species	Stage of Host	Parasite Species	Authority	Location
<i>Deltocephalus weedi</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Deltocephalus infumatus</i>	adult	?	F. A. F.	Corvallis, Oregon. F. H. L.
<i>Deltocephalus inimicus</i>	adult	<i>Gonatopus obscurisimus</i>	F. A. F.	Bay View and Columbus, Ohio.
<i>Deltocephalus inimicus</i>	nymph	<i>Gonatopus erythrodes</i>	F. A. F.	Castalia, Ohio.
<i>Deltocephalus abdominalis</i>	adult	?	F. A. F.	Katmai, Alaska. J. S. H.
<i>Deltocephalus affinis</i>	adult	?	F. A. F.	Bay View and Columbus, Ohio.
<i>Deltocephalus oculatus</i>	nymph	?	F. A. F.	Castalia, Ohio.
<i>Deltocephalus oculatus</i>	adult	?	F. A. F.	Castalia, Ohio.
<i>Deltocephalus balli</i>	adult	?	F. A. F.	Columbus, Ohio.
<i>Deltocephalus xanthoneurus</i> ?	nymphs	<i>Gonatopus pilosus</i>	Mik	Vienna, Austria.
<i>Deltocephalus silvestris</i>	adult	?	F. A. F.	Mt. Katahdin, Maine. H. O.
<i>Deltocephalus imputans</i>	adult	?	F. A. F.	Lexington, Tenn. D. M. D.
<i>Lonatura catalina</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Nephotettix</i> sp.	nymph	<i>Chalcogonatopus optabilis</i>	Perkins	Queensland, Australia.
<i>Nephotettix</i> sp.	?	<i>Gonatopus dubiosus</i>	Perkins	Queensland, Australia.
<i>Nephotettix plebius</i>	adult	<i>Gonatopus pulcherrimus</i>	Perkins	Queensland, Australia.
<i>Euscelis</i> spp.	adult	<i>Pachygonatopus melanias</i>	Perkins	Queensland, Australia.
<i>Euscelis</i> sp.	?	<i>Digonatopus koebelei</i>	Perkins	New South Wales, Australia.
<i>Euscelis</i> sp.	?	<i>Gonatopus pallidiceps</i>	Perkins	California.

Sub-family *Jassinæ*—Continued.

Host Species	Stage of Host	Parasite Species	Authority	Location
<i>Euscelis exitiosus</i>	adult	?	F. A. F.	Wellington, Kas. E. O., G. K.
<i>Euscelia humidus</i>	adult	?	F. A. F.	Houlton, Bog, Maine. H. O.
<i>Euscelis curtisii</i>	adult	<i>Gonatopus brunescens</i>	F. A. F.	Columbus, Ohio.
<i>Euscelis maritimus</i>	nymph	<i>Platygonatopus pedestris</i>	Dalman	Sweden.
<i>Eutettix</i> sp.	nymph and adult	<i>Chelognus nigricornis</i>	Perkins	Queensland, Australia.
<i>Phlepsius</i> sp.	?	<i>Chalcogonatopus pseudochromus</i>	Perkins	Columbus, Ohio.
<i>Phlepsius irroratus</i>	adult	?	F. A. F.	Covington, Tenn. D. M. D.
<i>Phlepsius truncatus</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Phlepsius apertus</i>	adult	?	F. A. F.	Houlton, Maine. H. O.
<i>Thamnotettix flavotinctus</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Thamnotettix crumbi</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Thamnotettix crumbi</i>	adult	?	F. A. F.	Columbus, Ohio.
<i>Chlorotettix unicolor</i>	nymph and adult	<i>Chelognus</i> n. sp.	F. A. F.	Castalia, Ohio, Corvallis, Ore. F. H. L.
<i>Chlorotettix nacreosus</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Chlorotettix galbanatus</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Chlorotettix necopina</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Cicadula lepida</i>	adult	?	F. A. F.	Clarksville, Tenn. D. M. D.
<i>Cicadula sexnotata</i>	adult	?	F. A. F.	Columbus, Ohio.

Sub-family *Typhlocybinae*.

Host Species	Stage of Host	Parasite Species	Authority	Location
Dikraneura sp.	adult	Aphelopus arizonicus	Perkins	Nogales, Arizona.
Dikraneura fieberi	adult	Aphelopus n. sp.	F. A. F.	Columbus, Ohio.
Empoasca smargdula	adult	Aphelopus n. sp.	F. A. F.	Marietta, Ohio. H. O.
Empoasca mali	adult	?	F. A. F.	Columbus, Ohio.
Empoasca flavescens	adult	?	F. A. F.	Columbus, Ohio.
Empoa commissuralis	adult	?	F. A. F.	Mary's Peak, Ore., F. H. L.
Erythroneura sp.	?	Aphelopus microleucus	Perkins	Nogales, Arizona.
Erythroneura sp.	?	Aphelopus pulcherzimus	Perkins	Nogales, Arizona.
Erythroneura tricincta	adult	Aphelopus sp.	F. A. F.	Kelley's Island, Ohio.
Erythroneura comes	adult	Aphelopus n. sp.	F. A. F.	Columbus, Ohio.
Erythroneura obliqua	adult	Aphelopus sp.	F. A. F.	Marietta, Ohio. H. O.
Erythroneura vulnerata	adult	Aphelopus sp.	F. A. F.	Columbus, Rockbridge, O.
Erythroneura douglasi	adult	Aphelopus melaleucus	Girard	France.
Erythroneura hippocastani	adult	Aphelopus melaleucus	Girard	France.

Genus or Species Unknown or Record Doubtful.

Jassid sp.	nymph	Chelogynus lusus	Perkins	Tucson, Arizona.
Jassid sp.	nymph	Chalcogonatopus rapax	Perkins	Nogales, Arizona.
Jassid sp.	nymph	Digonatopus plebius	Perkins	Java.
Large green jassid on oak	?	Deinodryinus paradoxus	Perkins	Nogales, Arizona.
Medium sized jassid on willow	?	Anteon arizonensis	Perkins	Nogales, Arizona.
Jassid sp.	nymph	Chelogynus funestus	Perkins	Tucson, Arizona.

FAMILY FULGORIDÆ.

Sub-family *Dictyophorinæ*.

Host Species	Stage of Host	Parasite Species	Authority	Location
<i>Thanatodictya</i> sp.	nymph	<i>Paradryinus</i> <i>javanus</i>	Perkins	Java.
<i>Hasta</i> <i>hastata</i>	nymph	<i>Paradryinus</i> <i>leptias</i>	Perkins	Queensland, Australia.

Sub-family *Cixinæ*.

<i>Cixius</i> <i>contaminatus</i>	?	<i>Lestodryinus</i> <i>formicarius</i>	Kieffer	Europe.
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Sub-family *Tropiduchinæ*.

<i>Vanua</i> <i>vitiensis</i>	adult	<i>Pseudogonatopus</i> <i>kiefferi</i>	Perkins	Fiji.
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Sub-family *Issinæ*.

<i>Brucomorpha</i> <i>oculatus</i>	nymph and adult	<i>Phorbas</i> <i>mirabilis</i>	Perkins	Columbus, Sandusky, Ohio.
<i>Brucomorpha</i> sp.	adult	<i>Phorbas</i> <i>arizonica</i>	Perkins	Nogales, Arizona.

Sub-family *Acanaloniinæ*.

<i>Acanalonia</i> <i>bivittata</i>	nymph	<i>Hesperodryinus</i> <i>amphiscepæ</i>	Perkins	Nogales, Arizona.
<i>Acanalonia</i> <i>bivittata</i>	nymph	<i>Perodryinus</i> <i>amoenus</i>	Perkins	Nogales, Arizona.
<i>Acanalonia</i> <i>immaculata</i>	?	<i>Apterodryinus</i> <i>torvus</i>	Perkins	Arizona.

Sub-family *Flatinæ*.

<i>Ormenis</i> <i>prunosa</i>	adult	<i>Psilodryinus</i> <i>arizonicus</i>	Perkins	Nogales, Arizona.
<i>Ormenis</i> <i>septentrionalis</i>	?	<i>Psilodryinus</i> <i>arizonicus</i>	Perkins	Nogales, Arizona.
<i>Ormenis</i> <i>septentrionalis</i>	adult	<i>Psilodryinus</i> <i>ormenidis</i>	Swezey	U. S.
<i>Misthanophan-</i> <i>tia sonorana</i>	nymph	<i>Hesperodryinus</i> <i>arizonicus</i>	Perkins	Nogales, Arizona.

Sub-family *Flatinae*—Continued.

Host Species	Stage of Host	Parasite Species	Authority	Location
Misthanophantia sonorana	nymph	Apterodryinus torvus	Perkins	Arizona.
Privesa aphrophoroides	?	Neodryinus raptor	Perkins	Queensland, Australia.
Privesa aphrophoroides	nymph	Paradryinus venator	Perkins	Queensland, Australia.
Scolypopa sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Gaetulia sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Siphanta sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Siphanta sp.	nymph	Thaumatodryinus koebelei	Perkins	Queensland, Australia.
Siphanta sp.	nymph	Paradryinus venator	Perkins	Queensland, Australia.
Siphanta sp.	nymph	Paradryinus threnodes	Perkins	Queensland, Australia.
Siphanta sp.	nymph	Paradryinus koebelei	Perkins	Queensland, Australia.
Siphanta sp.	nymph	Paradryinus varipes	Perkins	Queensland, Australia.
Sephena sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Colgar sp.	nymph	Paradryinus leptias	Perkins	Queensland, Australia.
Colgar sp.	nymph	Paradryinus threnodes	Perkins	Queensland, Australia.
Colgar sp.	nymph	Neodryinus nelsoni	Perkins	Queensland, Australia.
Colgar peracutus	nymph	Neodryinus koebelei	Perkins	Queensland, Australia.
Aphanophantia sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Massila sp.	?	Neodryinus raptor	Perkins	Queensland, Australia.
Masilla sp.	nymph	Paradryinus venator	Perkins	Queensland, Australia.
Massila sp.	nymph	Neodryinus koebelei	Perkins	Queensland, Australia.

Sub-family *Delphacinae*.

Host Species	Stage of Host	Parasite Species	Authority	Location
Stenocranus	?	Haplogonatopus vitiensis	Perkins	Fiji.
Stenocranus dorsalis	nymph	Pseudogonatopus stenocrani	Perkins	Ohio.
Perkinsiella saccharida	nymph and adult	Pseudogonatopus saccharatorum	Perkins	Queensland, Australia.
Perkinsiella saccharida	nymph	Echthrodelpfax fairchildii	Perkins	Hawaii.
Hadeodelphax	nymph	Echthrodelpfax nigricollis	Perkins	Queensland, Australia.
Hadeodelphax	nymph	Haplogonatopus moestus	Perkins	Queensland, Australia.
Aloha ipomeæ	nymph	Echthrodelpfax fairchildii	Perkins	Hawaii.
Pyrilla sp.	nymph	Lestodryinus pyrrillæ	Misra	India.
Pyrilla aberrans	nymph	Lestodryinus pyrrillæ	Misra	India.
Pyrilla aberrans	nymph	Chlorodryinus pallidus	Misra	India.
Pyrilla perpusilla	nymph	Chlorodryinus pallidus	Misra	India.
Pyrilla pusana	nymph	Chlorodryinus pallidus	Misra	India.
Pissonotes dorsalis	adult	?	F. A. F.	Orono, Maine. H. O.
Bostaera nasuta	nymph	Agonatopoides synchronous	Perkins	Nogales, Arizona.
Stobaera sp.	nymph	Pseudogonatopus arizonicus	Perkins	Nogales, Arizona.
Stobaera sp.	nymph	Pseudogonatopus autoxenobius	Perkins	Nogales, Arizona.
Liburnia sp.	?	Pseudogonatopus americanus	Perkins	Columbus, Ohio.
Liburnia sp.	?	Pseudogonatopus opacus	Perkins	Queensland, Australia.
Liburnia sp.	nymph and adult	Pseudogonatopus dichromous	Perkins	Queensland, Australia.

Sub-family *Delphacinae*—Continued.

Host Species	Stage of Host	Parasite Species	Authority	Location
Liburnia sp.	nymph	Pseudogonatopus perkinsi	Perkins	Hawaii.
Liburnia sp.	nymph and adult	Pseudogonatopus juncetorum	Perkins	Queensland, Australia.
Liburnia sp.	nymph and adult	Pseudogonatopus palustris	Perkins	Queensland, Australia.
Liburnia sp.	?	Pseudogonatopus kurandæ	Perkins	Queensland, Australia.
Liburnia sp.	?	Paragonatopus nigricans	Perkins	Queensland, Australia.
Liburnia sp.	?	Haplogonatopus brevicornis	Perkins	Queensland, Australia.
Liburnia sp.	?	Haplogonatopus apicalis	Perkins	Queensland, Australia.
Liburnia campestris	nymph and adult	Haplogonatopus americanus	Sweezey, Perkins	Columbus, Ohio.
Liburnia lutulenta	nymph and adult	Haplogonatopus americanus	Sweezey Perkins	Columbus, Ohio.
Liburnia verwandter	nymph	Echthrodelpfax nigricollis	Perkins	Queensland, Australia.
Liburnia verwandter	nymph	Echthrodelpfax bifasciatus	Perkins	Queensland, Australia.
Dicranotropis sp.	?	Pseudogonatopus nudus	Perkins	Java.

Genus and Species Unidentified.

Aphanophantia ?	nymph	Paradryinus koebelei	Perkins	Queensland, Australia.
Siphanta ?	nymph	Chloridryinus pallidus	Perkins	Queensland, Australia.
Fulgorid species	?	Antonella robusta	Dodd	Queensland, Australia.
Fulgorid species	?	Antonella bicolor	Dodd	Queensland, Australia.

Twenty-two genera, including forty-nine known species and five unidentified ones out of three of the six sub-families in the *Cicadellidæ* are known to be parasitized by the dryinids. Most of the host records are in the sub-family *Jassinæ* chiefly grass living forms. In the *Fulgoridæ*, twenty-six genera, including twenty-two species and four unidentified species are known to be subject to parasitism by these insects. In this family most of the host records are in the sub-family *Delphacinæ*. In all fulgorids the nymphal stages are the most susceptible to attack, the only adults parasitized being the weaker and less active forms. It is likely that nearly every species in these two families is subject to attack by one or more species.

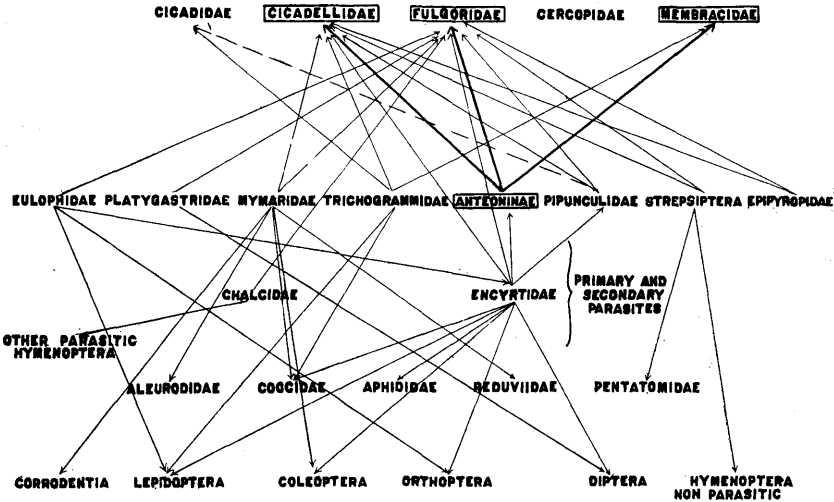


DIAGRAM 1.
Interrelations of *Anteoninae* with other parasites.

The above diagram represents graphically the inter-relations of the *Anteoninae* and their hosts with other related parasites of these hosts. It is seen at once how small a part they play as a group in comparison with the other parasites in maintaining nature's balance. They are but one link in a very complex series. The leaf hoppers are parasitized also by the *Eulophidae*, *Platygastriidae*, *Myrmariidae*, *Trichogrammidae*, *Chalcididae*, and *Encyrtidae* of the *Hymenoptera*, by the *Pipunculidae* of the *Diptera*, by the *Epipyropidae* of the *Lepidoptera*, and by the

Strepsiptera. In addition to parasitizing the *Homoptera*, the *Anteoninae* are themselves parasitized by the *Encyrtidae* and *Eulophidae*.

Aside from parasitizing the *Homoptera* most of the groups mentioned attack such other insect groups as the *Hemiptera*, *Coleoptera*, *Diptera*, *Orthoptera* and *Hymenoptera*. In comparison with the other groups it is noted that the *Anteoninae* and *Pipunculidae* are narrowly restricted in their range of hosts.

BIOLOGY AND LIFE HISTORY.

Adult.—The adult dryinids are found living in grasses, herbage and trees, in fact wherever their hosts, the leaf- and tree-hoppers, are found. The females are much more active, continually running and flying about in search of their prey. In species where the female is wingless, the habits of the two sexes are very different, the males generally being found resting on the leaves and stems, or flying about in search of the females. In describing the habits of *Lestodryinus* (*Dryinus*) *pyrillae* Kieffer, Misra (1917) says: "The adult females are very active and may be seen actively flying about the leaves, occasionally settling down, especially near the nymphs, and then flying away. The adults are prominent mostly during the hottest part of the day." Later in the same paper, speaking of *Chlorodryinus pallidus* Perk., he says: "It is the female which is mostly in evidence in the fields when the leaf-hopper is present in numbers on the canes. The male is rarely seen about the infested fields."

Not all winged dryinids are as active as Misra has observed, for Perkins (1905) says: "The prey is sought on foot, for while most of the *Anteoninae* (*Dryinidae*) are most active and rapid runners, they are but poor performers on the wing. In most of the winged forms, these organs are unduly short, and in *Echthrodelpfax* serve hardly more than to transport it from one cane plant to another as occasion demands." There seems to be no correlation between the presence of wings in this family and the habit of attacking arboreal hoppers. Perkins (1905) noticed that in Australia and generally in America, the apterous forms of the *Gonatopus* type preyed upon hoppers that fed on grasses and low herbage. "On the other hand," he says, "the Hawaiian apterous species are essentially arboreal."

Mimicry.—Along with the loss of wings in the female, there has been developed the remarkable resemblance to ants in many forms. This has been adaptive and due entirely to the mode of life of the female. Not only have the wings been lost, but the legs have been modified for running, and the forelegs especially for grasping the prey. Thus the thorax has become greatly modified and more closely fused with the propodeum. In the more highly specialized species, many of the thoracic sutures have been obliterated and segmentation of the thorax is indistinct. The latter is divided into two nodes by the narrow mesonotum, and may even be divided into three nodes. This division of the thorax and the pedunculate form of the first abdominal segment are adaptations to the stinging habit of the female, enabling her to bend the entire body in an arc while stinging the prey.

Many species have evidently taken advantage of this ant-like form and are frequently found associated with ants, sometimes being found in the nests of the latter. This association in the case of *Platygonatopus pedestris* (Dalm.) was observed by Haliday in 1834, when he says: "The first time I met with this species, it was in company with some *Myrmicæ* (not *M. rubra*), under a stone, in a chalky lane. * * * In this island, its haunts are on the sand-hills of the coast, among which *Formica emarginata* swarms. The *Dryinus*, which is not dissimilar in form and color, moves among them distinguished by its hitching gait, produced by the enormous length of the tarsi and trochanters of its forelegs; it can run pretty fast, however. * * * I witnessed an occurrence which shows that it is not always quite amicable. Four ants were bearing off one of the *Dryinii* quite alive and vigorous, though not able to struggle much in their grip; my approach disturbing them, three scampered off, but the fourth, more determined, held on; the *Dryinus* however, as soon as she got fair play, showed fight, and though her small jaws seemed ill calculated to match those of the ant, the battle was maintained without any visible disadvantage. * * * " Perkins (1905) says that "*Paranteon* no doubt has special habits; for the sluggish hopper that it affects, forms flocks of greater or less extent, and excreting much honey dew, is invariably covered with swarms of ants, usually a moderate-sized species of *Formicidæ*. The *Paranteon* bears some slight resemblance to the ant in appear-

ance, and this resemblance is enhanced by its actions. If a number of parasites be bred together in a glass vial, they may be seen gathered in pairs, standing sub-erect on their four hind legs, face to face, stroking one another, licking each other's mouth, soliciting food. Now the ants that attend the hoppers themselves behave in a similar fashion, and it is most probable that they actually feed the *Paranteon*, which unless it were on friendly terms with the ants, could never approach the hoppers to lay its eggs in these. * * * Further, it would be interesting to note what happens to the full-grown larva of the parasite, which must emerge from its sac amongst a swarm of carnivorous ants that are always prepared to kill and carry off any weaker insect that falls in their way. Most probably not only are the larvæ not harmed by the ants, but they may be carried down by them to their underground nest, and pupate therein."

There are several records of dryinids being collected in ants' nests. The following species have been recorded as associated with ants: *Dicondylus distinctus* (Kief.), England, in colony of *Myrmica*; *Dicondylus striatus* (Kief.) Austria and England, in nest of *Formica fusca*; and *Gonatopus Myrmecophilus* (Kief.), Luxemburg and England, with *Formica rubibarbis*.

Apterous species are often collected by turning over stones, and are very rarely reported as being taken in the net, although this may be due to their close resemblance to ants.

Both sexes feed readily on water sweetened with sugar. Perkins (1905) noticed individuals of *Echthrodelpfax* feeding on the honey-dew secreted by their host, a certain fulgorid. They may attack and devour their host, for the same author says that "under unnatural conditions, such as in the confinement of a small jar or glass tube, and probably under pressure of hunger, the hoppers are frequently killed outright, and to some extent devoured." In the act of oviposition, the female invariably works her mandibles on the cuticle of the hopper, and sometimes produces a wound which in some cases so weakens the hopper as to cause its death. Again no sign of a wound is noticed after oviposition.

The longevity of the adults varies with the sexes, the female invariably being much the longer lived. In fact, the males live often but a few days, often only for a day. Frequently, according to Perkins (1905), the male dies after copulation. The female may live as long as seventeen days in captivity, and undoubtedly much longer under natural conditions.

In the species studied, the act of pairing was unobserved. In spite of the fact that with *Gonatopus erythrodes* (Perkins) and *Haplogonatopus americanus* (Perk.) males and females were placed together for observation under as natural conditions as possible, neither sex paid any attention to the other. The females were constantly running around among and over the grass-blades as if searching for their prey. On the other hand, the males were as a rule inactive, resting upon the sides of the cage or on the grass leaves. Perkins (1905) concerning *Echthrodelpfax*, states that "pairing of the sexes is of short duration, and after copulation the male frequently never moves again, and in general dies very quickly."

Parthenogenesis occurs probably to a considerable extent in this sub-family. This has been proven in captivity, and undoubtedly occurs to some extent under normal outside conditions. The great disproportion of sexes in some species, and the fact that with others males have not been found, seems to bear out that statement. In commenting on *Pseudogonatopus* Perkins (1905) says that but one in forty adults was a male. Males have not been either captured or bred from species of *Eugonatopus* or *Agonatopus*. Adults from unfertilized eggs of *Gonatopus contortulus* Patton were all females, and were normal and active in every way.

Polyembryony has been recorded for this group in the case of *Aphelopus theliae* Gahan ms. parasitic on *Thelia bimaculata*.

The method of attack and oviposition is very similar for nearly all species of the *Anteoninae*. Upon nearing the prey the female comes to a standstill, throwing her antennæ backward and swaying from side to side before making her jump. She then throws herself upon the hopper, which may escape by a quick jump. The chelate claws of the forelegs are thrust out at the same time, and the prey is seized in this manner. Once the hopper is captured, the female grasps it with all six legs, and placing her body sidewise across that of the struggling host, curls the tip of the abdomen under and thrusts the sting in the ventral side of the thorax in the case with *Gonatopus erythrodes* (Perk.) and *Haplogonatopus americanus* (Perk.) as observed by the writer, and with *Echthrodelpfax* as noted by Perkins (1905). With *Gonatopus contortulus* Patton, however, the host is large and robust and winged, so that the method of attack is varied. Here the prey is stalked from behind, and

while clinging to it with the front pair of legs, the sting of the dryinid is thrust forward beneath her body and into the ventral side of the abdomen of the jassid. If the latter jumps, both fall to the ground; and in this case the process of stinging is similar to the above-mentioned species. With other species the sting is thrust in different places on the host, according to various observers. While the hopper is struggling, the parasite may be seen trying to locate a vulnerable spot in its host's armor. This always seems to be in the thin membrane separating adjacent segments. Once stung the hopper is paralyzed, and it is then dragged to a convenient place for oviposition. In several instances the parasite dragged the stunned jassid around the vial for some time before stopping to oviposit. In doing this the mandibles are used, the wasp backing around, dragging the host after it. In many cases the host was oviposited in immediately. In the case of opaque nymphs, before the ovipositor is inserted, the sting can be seen working this way and that with extreme rapidity, just beneath the cuticle. It is finally withdrawn, and the ovipositor thrust in deeply into the body of the nymph, and the egg laid. The entire operation extends from one to often two or three minutes.

In *Gonatopus contortulus* Patton the egg may be laid on the outside of the cuticle, although it is more often thrust beneath it. In a *Gonatopus* species parasitic on *Deltocephalus inimicus* nymphs, the egg is thrust down between the segments, the tip just protruding outside.

Perkins (1905) remarks that "occasionally after capture, the prey is released without being stung, and that it is probable that hoppers so released have already been stung by an earlier captor." The writer is inclined to doubt this as the real explanation, since more than one larval sac is often found on one host. Once a nymph was found bearing a nearly mature larval sac and an egg just protruding externally between the segments. As there was only enough food present in this nymph for the maturing of but one parasite, the fate of the youngest dryinid is obvious. It is evident that it is just a matter of chance whether the captured nymph has been previously parasitized or not, and that when the female does not oviposit the cause must be something other than that of previous oviposition.

In some species there is just enough food present in the hopper to feed but one dryinid, while others may be seen bearing from two to as many as eight parasites. In fact, with *Brucomorpha oculatus*, two or three parasites are more often found attached than one, and these may all mature if the host is a large, robust individual. Generally the parasites on a hopper are of one species, but may be of two different species. One sex seems as readily attacked as the other. Some species confine their attacks entirely to nymphs, others to adults, and others to both nearly mature nymphs and adults. Once a nymph is parasitized it never becomes adult, in so far as observed by the writer. Keilin and Thompson (1915) state that the *Typhlocybidæ* parasitized by *Aphelopus malaleucus* Dalm. are oviposited in before becoming adult. With *Erythroneura tricincta*, parasitized also by a species of *Aphelopus*, adults have been kept in captivity as long as a week before a sac appeared externally. It would seem, then, that with this species the egg is laid after the host becomes winged. Nymphs parasitized by *Gonatopus* and its allies never become adults, no matter if they are in their last instar. *Gonatopus erythrodes* (Perk.) attacks nymphs in the second, third and fourth instars, but prefers nymphs of the fourth instar. The place selected for oviposition with a given species of dryinid is generally restricted not only to either the abdomen or thorax, but also to certain segments of these, or in certain positions on these segments, as, for instance, with *Haplogonatopus americanus* Perk. Its sacs are found invariably protruding dorsally between the last two or three abdominal segments. Very often a species of dryinid confines its attacks to one species of hopper. Others may parasitize closely-related species; and still others may parasitize species in different genera.

After oviposition the dryinid drops the hopper and runs away. The latter recovers rapidly, and generally within five minutes recovery is complete and feeding is resumed. The number of eggs a female may lay is probably considerable, though not as large as with many hymenopterous parasites. In captivity the largest number of eggs obtained was thirteen, and the greatest number in a single day was six. These figures are unquestionably much too low for normal conditions. The females are ready for oviposition as soon as they have fed after emergence, so that the oviposition period must extend through-

out the entire period of adult life, probably a month in nature. Basing the above number of eggs per day on this period of oviposition, the maximum number of eggs that can be laid is one hundred and eighty.

Egg.—Since the egg is very minute and often is thrust down deeply into the body, it is practically impossible to locate it either by dissection or by sectioning the host. For this reason, the date of hatching is still in doubt, and the incubation period can only be estimated from the time the egg is laid to the appearance of the sac outside the body-wall of the hopper. In *Gonatopus erythrodes* (Perk.) a blackish discoloration precedes the appearance of the sac by several days, and is noticed five days after oviposition. Since in this case the discoloration is due to the black sac beneath the cuticle, the egg must have hatched within two or three days after being laid.

Larva.—The earliest stages of the dryinid larva have been described by Keilin and Thompson (1915) for *Aphelopus malaleucus* Dalman parasitic on *Erythroneura* (*Typhlocyba*) *hippocastani*. They report finding an embryonic stage within the tissues of the host, and do not consider it as the first larval stage. The exact relation of this "embryo" to the first stage larva is not known. It is possible that this may be the true first instar, which may be modified and different from the following ones. In case the egg is internal, just previous to emerging from the host, the larva is seen to be curved into the form of a U, the apex of which appears first between the segments. This is the second larval stage, and it is covered almost entirely and protected by the exuvium of the first instar. The appearance of the sac externally on the host takes place in from five to seven days after oviposition. During this time the egg has hatched, the "embryonic" stage has been passed, and a molt has taken place.

The second molt occurs in from five to ten days after the emergence of the sac, and is indicated by the rupturing of the first exuvium along a median dorsal line. Between the gaping halves of this split, the second exuvium is gradually pushed outward by the growth of the larva within, now in its third instar. Accompanying this split there is often a change in the coloration of the sac, as from dark green to black.

As growth occurs, the second exuvium becomes split open in the same manner as did the first, a fact coincident with a third larval molt, and the third exuvium is pushed outward by the larva, now in its fourth instar, exactly as before. The fourth larval stage is not comparable to the other four. It is characterized by the development of the mandibles, beneath which are formed those of the fifth stage. There is no complete fourth molt, so far as is revealed by dissections, other than a shedding of the head capsule. It is possible that this instar is entirely eliminated in some of the more highly specialized species. The larval sac has become of considerable size by now, and is plainly visible on nymphs and brachypterous forms. In winged species, the sac pushes one wing and elytron up out of place. The host becomes very evidently affected by now, being sluggish and easily caught. In from eighteen to nineteen days after the appearance of the sac the fourth partial molt occurs, and the larva enters upon its fifth and last larval instar. Up until this time it has not touched any vital part of the host. The mouth-parts of all the preceding instars are soft and slightly chitinized, while in this last stage, sharp, heavily chitinized mandibles are developed and the tissues of the host are devoured. Growth is now very rapid, and soon the larva breaks through the sac, first being seen as a narrow white band between the slightly gaping halves of the exuviae. Peristaltic-like movements take place spasmodically in the maggot, which increases visibly in size. In the case of *Gonatopus erythrodes* (Perk.) parasitic on *Deltocephalus inimicus* nymphs, the last stages are easily studied as the host is not very heavily chitinized and opaque yellow in color. The dark jaws of the parasite can be seen working in the interior of the host's abdomen first. The entire abdomen is emptied of its contents before the parasite directs its attention to the thorax. At this time, an hour after the last molt, the hopper is still alive and responds to stimulus, but it now dies very quickly as soon as the thoracic viscera are attacked. The feeding seems to be a combination sucking, in which the cone-like labium functions and the cutting by the sharp mandibles. The head is attacked after the thorax, and soon there is nothing left of the hopper but a mere shell. The contents of the host seems to be partially liquified at the final stages. About two hours elapse between the final molt and the consumption of the host.

. Coincident with the growth of the parasite is the formation and development of the sac. (Figs. 1-7). When the larva hatches it is generally entirely or almost within the body of the host and surrounded by its tissues. As it grows it gradually assumes a curved position, due either to unequal growth or pressure against the host's tissues. It also pushes its way along the path previously made by the ovipositor toward the external point of insertion of the latter. If the egg is laid internally, it undergoes its first molt still within the body of the host, as

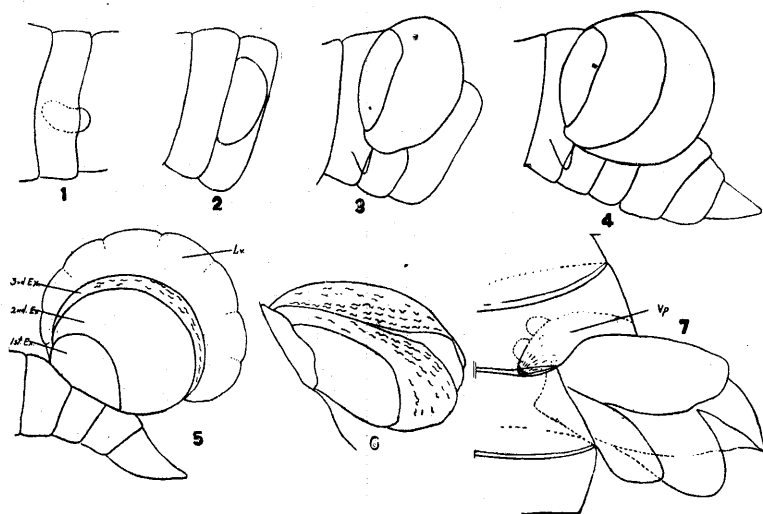


FIGURE 1.

1-6, side view of abdomen of *Deltocephalus inimicus* nymphs, showing stages in parasitism by *Gonatopus* sp.; 1, egg; 2, second instar; 3, third instar; 4, fourth instar; 5, fifth instar; 6, empty sac; 7, dorsal view of abdominal segments of *Deltocephalus sayi* adult showing empty sac of *Gonatopus* sp.; 1st, 2nd, and 3rd. Ex., first, second and third exuviae; Lv., larva; Vp., ventral larval process.

noted; and instead of entirely breaking through the exuvium dorsally in the normal manner, it splits the latter ventrally and uses it as a buffer in forcing its way outward. It becomes more and more curved in position, and finally breaks through the cuticle of the hopper still with the protection of the first exuvium, which surrounds it as a sort of hood. At no external point, then, is the larva exposed, but with its head and caudal end still in the tissues of the host, it feeds and the first exuvium becomes fused with the cuticula of the hopper by a series of chitinous hooks or other means. At the second molt, the second exuvium

is split ventrally as was the first, and it is pushed outward by the growth of the third instar within, breaking through the first exuvium which is firmly attached to the host. This process is repeated in the third molt, the second exuvium becoming split open by the third. The exuviae become chitinized and darken in color in some species. In *Phorpas mirabilis* (Perk.) parasitic on *Brucomorpha oculatus*, this darkening and hardening of the exuvium begins in the region of the spiracles, and at first there is on each segment an oval black spot around each. These later become confluent and it seems that apparently after the skin is shed the air has something to do with the hardening of the exuvium. The exuvium just shed also adheres very closely to the growing larva which at first breathes through the spiracles of this cast skin. Tracheae can be seen in direct connection between the first pair of spiracles, even in the late phase of this instar. Just before the fourth molt, then, there is present the fourth instar parasite larva, protected dorsally by the third exuvium and laterally by the first and second. During the late phases of the second instar, the parasite pushes itself completely outside of the host, remaining attached by the chitinous ring of the sac only, and with its head and posterior extremity just within the body of the hopper. Later on the head alone remains within the body of the host.

With the final consumption of the host, the maggot withdraws its head from within the shell of the latter, which it quits, and goes off in search of a place to spin its cocoon. In some species the dead shell of the host is jerked abruptly away by the maggot (Misra, 1917). The larva is quite active, and crawls around on its back similar to a *Cotina* grub by peculiar peristaltic like movements, originating at the caudal end as a constriction which progresses anteriorly. Sometimes as long as a day is spent before the cocoon is started, and again it is begun almost immediately, even beneath the dead host (Swezey, 1903). The cocoons are spun either beneath the soil or above it on leaves or other objects. Sometimes there is variation in individuals in regard to the location of the cocoon. The first generation cocoons of *Gonatopus erythrodes* (Perk.) were spun below the soil, but some of these of the second were spun above the soil on the sides of the cages. The cocoon is completed in from one to two days, although larvæ that are to pass the winter may be seen lining their cocoons for days after they are apparently finished.

Pupa.—Directly after completing the cocoon, the larva becomes quiescent, and within one or two days assumes a straight, rigid shape, becoming a prepupa. After five to seven days pupation occurs, the larval skin being pushed down into the bottom of the cocoon as a tiny crumpled mass. The time spent in the pupal stage varies greatly—from three to five weeks with different species. At the end of this time, the adult issues, but does not as a rule emerge from the cocoon until two or three days later. It then chews its way out at or near one end, and is ready for active life immediately. The total life cycle varies from a year to as low as forty-three days.

SEASONAL HISTORY.

Hibernation.—All species of the dryinids studied by the writer have so far passed the winter as larvæ within the cocoon; and this is probably true of the great majority of them. A few got as far as the prepupal condition, but all larvæ collected in September and late August remained as such. There seems to be no difference in the structure of the winter and summer cocoons.

Generations.—The number of generations a year depends upon the species of host attacked, and of course upon the climate. Species attacking a host that has two generations a year—as with *Gonatopus erythrodes* (Perk.) parasitic on *Deltocephalus inimicus*—have the same number of generations. Others have but one. Two generations a year seems to be the maximum in this latitude, though farther south there are probably more. When a species attacks but one stage of its host, it must spend most of the year in the cocoon, issuing only when the right stage of its host is present. In one case, that of *Chelogenus chlorotettixi* n. sp. parasitic on *Chlorotettix unicolor*, the nymphs of which are found only in June in the Lake Erie region, spins its cocoon in early July and remains as an active larva within its cocoon throughout the remainder of the summer until the next spring, when it pupates and emerges in June in time to attack the nymphs of its host. One cocoon of this species was carefully split open in September, and an active white larva revealed. Later it was noticed that this larva had spun over the slit in its cocoon.

In some cases, where there are two generations a year, part of the larvæ of the first will pupate and the rest will remain

as larvæ until the following spring. A similar instance was noticed by Perkins (1905) in the case of estivating larvæ. He says: "The number that remain as larvæ, when others emerge after the usual period, may amount to not less than twenty-five per cent." From two thousand cocoons of (*Dryinus*) sent to Perkins in Hawaii from North America and arriving there in November, two males emerged a few weeks after arrival, and one male a month later. After being removed to a cooler and damper place, both sexes issued in a short time. This retarding of development is characteristic not only in localities where winters are long and severe, but also where a hot, dry period is experienced. It is a phenomenon that has been noticed with other insects, and is a means probably of insuring a continuance of the species in case the immediately following generation is not successful and perishes for want of food.

DESCRIPTION OF STAGES.

EGG.—The egg of the *Gonatopus* species studied (Figs. 8 and 9) is either oval or kidney-shaped, and varies in color from light yellow to dark grey or dark brown. In length it averages from .15–.211 mm. and in width from .08–.095 mm. There is no sculpturing on the chorion of any studied and in the case of those laid within the body of the host, no surface structures. In one egg, that of a *Gonatopus* species on *Deltocephalus inimicus* nymphs, a circular ridge, hardily visible, was noticed at one pole, and a black excrescence about half way down on one side. When laid on, or partly exposed on, the cuticula of the host it may be of the same color and almost invisible, as in *Gonatopus contortulus* Patton, or its color may be sharply contrasted with that of the host.

LARVA: *First instar*.—The earliest stage found was that of a larva within its egg shell ready to hatch (Fig. 10). It was structureless, with no visible appendages or segments. A small dark brown spot present at one extremity might serve for the purpose of breaking open the egg chorion, which is comparatively hard and thick.

Second instar.—The second instar of *Aphelopus comesi* n. sp. was studied, (Fig. 11). The specimen observed measured .54 mm. in length and .23 mm. at its greatest breadth near the head region.

The posterior third of the body is flexed downward and forwards, the anal extremity pointing cephalad. Two lobed processes projecting dorsally from the cephalic region are the

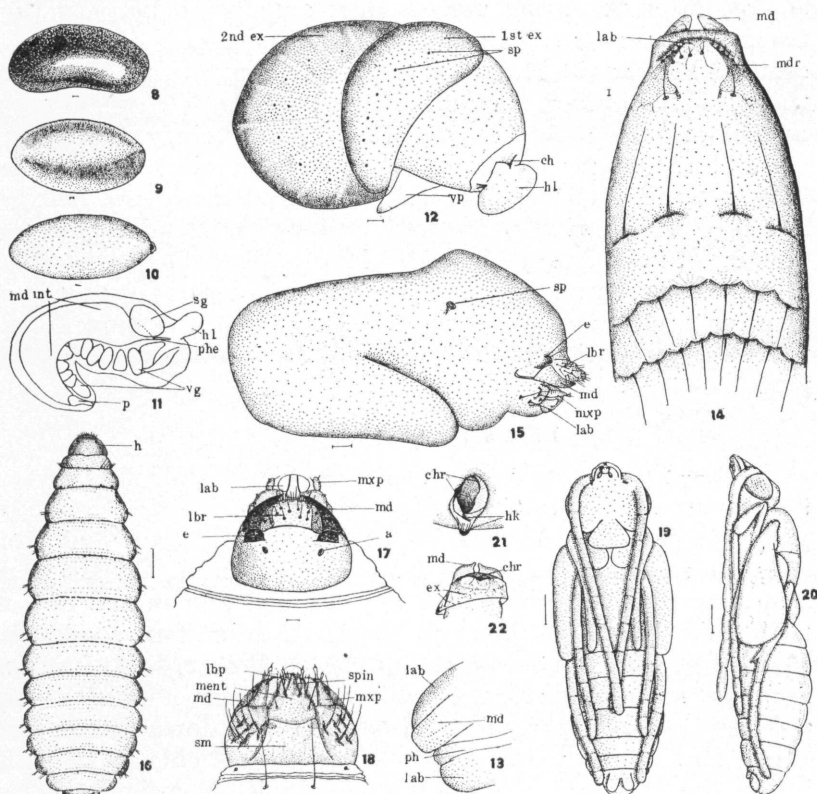


FIGURE 2.

8, egg of *Gonatopus* sp.; 9, egg of *Gonatopus erythrodes* (Perk.); 10, first instar of *Gonatopus erythrodes* (Perk.); 11, second instar of *Aphelopus* sp.; 12, third instar of *Gonatopus contortulus* Patton; 13, side view of mouth parts of fourth instar of *Anteón* sp.; 14, dorsal view of fourth instar of *Gonatopus* sp.; 15, fifth instar of *Gonatopus contortulus* dissected from sac; 16, dorsal view of mature larva of *Gonatopus* sp.; 17, dorsal view of head of *Gonatopus* sp., mature larva; 18, ventral view of head of *Aphelopus* sp., mature larva; 19, ventral view of male *Haplogonatopus americanus* pupa; 20, side view of same; 21, cavity in body wall of *Erythroneura comes* produced by *Aphelopus* sp.; 22, dorsal view of head of *Aphelopus* sp., fourth instar showing relation to larval sac, and chitinous ring. 1st, 2nd., and 3rd. Ex., first, second and third exuviae; Vp., ventral larval process; md. int., mid intestine; sg., supra-esophagial ganglion; hl., head lobe; phe., pharynx-esophagus; vg., ventral nerve chain; p., proctodeum; h., head; spin., spinneret; ch., chitinous head process; e., eye; lbr., labrum; md., mandible; mxp., maxillary palp; lab., labium; a., antenna; lbp., labial palp; sp., spiracle; ment., mentum; sm., submentum; ph., pharynx; mdr., developing mandibles.

only mouth parts. A large mid-intestine beginning just back of the head extends throughout the greater length of the body to near the anal end. The pharynx-esophagus is a very narrow tube, distinguished below the supra-esophagial ganglia. The hind-intestine is contiguous with the mid-intestine, but there is no connection between the two. In *Aphelopus melaleucus* Dalm., according to Keilin and Thompson, the salivary glands are very long and have a winding course. They were not seen in the specimen studied by the writer. Twelve ventral ganglia are easily distinguishable, the two anterior of which are doubtless thoracic and cephalic. The second is connected with a more or less elongated ganglion located just ventral to the first or sub-esophagial ganglion. The above mentioned authors report finding fourteen ganglia in the ventral nerve chain of *Aphelopus melaleucus* Dalm. instead of twelve, which is the ordinary number in other Hymenopterous larvæ. Nine pairs of spiracles are present in this stage.

Third instar.—In this stage the larva assumes a more marked curved position, being bent ventrally in the form of a U, the cephalic and caudal ends being approximate, (Fig. 12). The head and anterior third of the body lie buried in the tissues of the host, the rest of the larva protruding externally. It is completely enclosed in the second exuvium, except the head region. The first exuvium lies midway across each side of the body. In some species the ventral portion of the body immediately back of the head is prolonged into a peculiar appendage, which is enclosed by a cone-shaped membrane, the cuticle of the second exuvium. This is turned outwardly and posteriorly and its tip lies just beneath the chitin of the host at the juncture of two metameres, and is often visible externally in the case of light colored nymphs as a dark brown process extending under the cuticula from the point of attachment of the parasite. Often there is no corresponding larval tissue within this and in this case a small opening is noticed at the tip. It may serve to tap the outside air and thus keep a supply under the second exuvium for the enclosed larva. There is no connection between the spiracles of the second exuvium and the larva unless the thoracic pair retain this as they do in the next stages. The mouth parts are similar to those of the preceding stage except that they are larger. In *Gonatopus contortulus* Patton they appear as two oval, fleshy lobes projecting prominently from the head

region. At their bases the head is constricted visibly and at this constriction there are four triangular chitinous processes. These lobes may represent the mouth parts alone and may also be considered as the rudiments of the head. They are very firmly embedded in the tissue and are often detached and overlooked. Eleven distinct ganglia of large size comprise the ventral nerve chain, the first two being the largest. Beneath the second exuvium the cast tracheae and their branches can be seen. Nine spiracles are present.

Fourth instar.—The exact status of this stage is not yet determined. It is indicated only by the characteristic mouth parts, (Figs. 13 and 14), and the exuvium has not been noticed if indeed there is more than a molting of the head parts. It is obvious that the change from the peculiar soft lobed mouth parts of the third instar to the heavy chitinized mandibles of the last instar is too abrupt and that there must be an intermediate stage probably having been mostly suppressed with the specialization of the group. The mandibles in this stage are distinct curved processes with broad rounded and notched tips, thinly chitinized. A simple truncate labrum is present. Shortly after this stage has been reached the fifth instar mandibles develop back in the head, the point of each projecting into the base of the fourth instar mandibles. This instar is not represented by any of the three exuviae composing the larval sac.

Fifth instar.—Shortly before the appearance of the larva from the larval sac the mouth parts of the last instar are completely developed, and larvæ dissected out of sacs showing the three larval exuviae present the same type of mouth parts as the mature free-living larva, (Fig. 15). Though fully developed late in the preceding stage the cutting mandibles do not function until this instar. The mouth parts are represented by the rounded labrum, the dark brown, curved, sharply pointed mandibles, the maxillae, and labium. Just dorsal to, and at the base of, the mandibles are the irregular pigmented eye spots. Nine spiracles are present, the first pair being of large size and brown color and situated back of the head on the second thoracic segment. All the other spiracles are indistinct. The body still retains the U shape, though now the anal extremity reaches only as far as the first or second thoracic segments. If the mature larva is hairy as in the case of *Aphelopus* species,

the hairs can be seen resting back along the body, those of the first segment pointing cephalad, those of the rest caudad. In some species the peculiar cone-like structure is still present in this stage. This is evidently peculiar to only those species ovipositing in the abdomen of the host and it is characteristic of at least four stages since in nearly mature larvæ a series of four, all telescoping more or less within each other, can be seen. It has been found in parasites ovipositing in the abdomen of *Chlorotettix unicolor* nymphs, *Deltocephalus inimicus* nymphs and adults, and *Deltocephalus sayi* adults.

While in the sac the head of the dryinid larva is always ventral and the caudal end of the body is curved upwards and anteriorly lying dorsal to it. The spiracles of all the exuviae are open, but are not connected in any way with those of any of the larval spiracles. However, a trachea can be seen running from the first spiracle of the third exuvium to the corresponding spiracle of the larva itself, so that it is possible some air may be taken in by the parasite in this way. The fifth instar is enclosed laterally by the three exuviae and dorsally by the third only.

Mature Larva.—The mature larvæ vary in size, those studied measuring from 1.5 mm. to 4 mm. in length. They are blunt and wider posteriorly and more pointed anteriorly (Fig. 16). They are variously colored, agreeing in many cases with the color of their hosts. They may be various shades of green and even light pink, but as a rule they are white. *Aphelopus* larvæ are quite pubescent, but those of the more highly specialized types are almost without hairs. The head is distinctly separated from the body and is light brown or grey in color. Thirteen segments are visible not including the head. They are more or less concealed by the folds in the skin. On the head (Figs. 17 and 18) dorsally the two black pigmented eyes, the rudimentary antennæ and the short arcuate labrum are visible. The former may be but slightly pigmented and very indistinct, even in a species that normally has pigmented eyes. The labrum is covered with short spines and appears as a fleshy projection from the side. The curved heavy mandibles are very prominent. They are one-jointed and articulated from a chitinized basal piece. In *Neodryinus* and *Paradryinus* the cutting edge is crenulate or denticulate (Perkins, 1905), or it may be notched in *Gonatopus* (Mik, 1880). The maxillæ are less distinct. Laterally they are represented as short truncate

fleshy lobes from which project the short one-jointed maxillary palpi. The latter bear at their ends two minute papillæ, each with a spine at the tip. The labium is large and very prominent. From the side it is seen as a fleshy elongated process with a distinct apical half cut off from a broader basal piece. The basal piece or sub-mentum of the labium extends nearly back to the posterior margin of the head. To it is attached the mentum which extends just beyond the tips of the mandibles and bears at its tip a semi-circular transparent organ. A narrow triangular piece is attached about half way back on the ventral side of the mentum and projects to the tip of the labium. It is the spinneret and at either side of this the small one-jointed labial palpi are attached.

The pair of thoracic spiracles are nearly concealed under a fold in the integument and the others are very small and usually not visible. All the abdominal segments except the last two bear a pair of spiracles, there being ten pairs in all.

PREPUPA.—After spinning the cocoon the larva soon becomes quiescent and shrinks down into the lower half of it. Within a few days it becomes straight, rigid, extending the length of the cocoon, and constricted near the middle. After assuming this position it soon pupates.

PUPA.—The pupa (Figs. 19 and 20) is white, all the parts of the adult insect being plainly distinguished. If the adult is winged the wing pads are large and extend the length of the thorax to the first abdominal segment. Seven abdominal segments are visible. Pigmentation begins in the compound eyes and gradually spreads over the entire body the pupa becoming black before the adult issues.

LARVAL SAC.—As previously stated the larval sac is merely the cast skins of the larva itself modified for protective purposes by being more or less chitinized, and firmly attached to each other and to the host. The means of anchoring the sac to the host varies in different genera. In *Aphelopus* this attachment consists of a sort of chitinous ring and two hooks, (Figs. 21 and 22). One of the latter is smaller, sharply pointed, and strongly chitinized, the other is larger, blunt and but thinly chitinized. The chitinous ring serves to keep the cuticula of the host open, thus affording a place for the head and mandibles of the parasite.

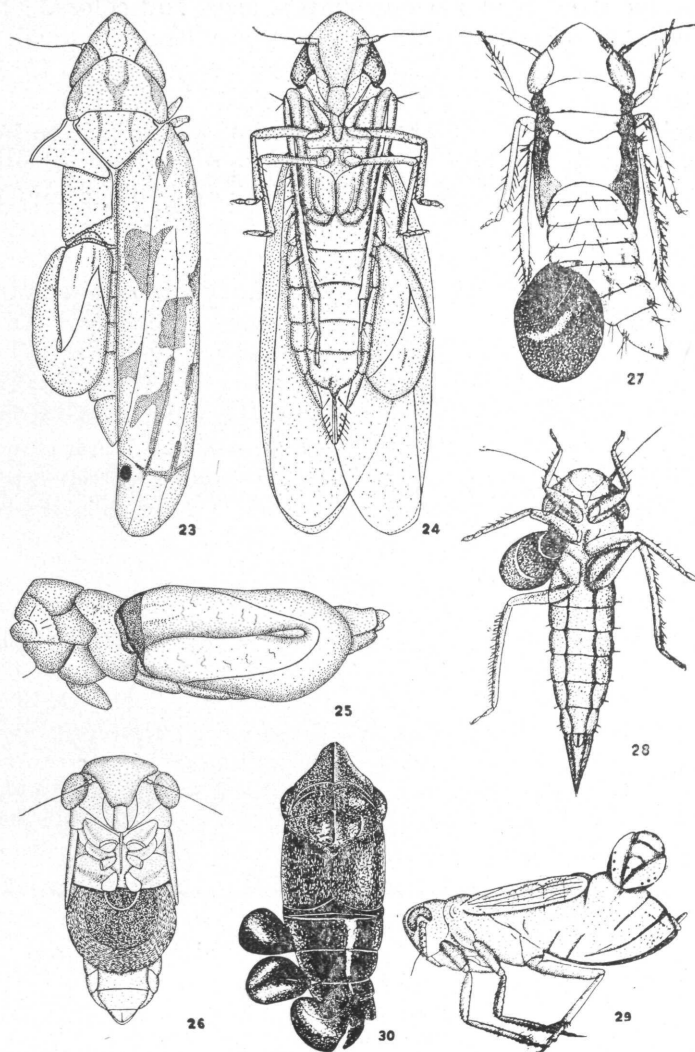


FIGURE 3.

23-25, dorsal, ventral and side views of *Erythroneura* comes parasitized by *Aphelopus* sp.; 26, ventral view of *Agallia sanguinolenta* parasitized by *Anteon* sp.; 27, dorsal view of *Deltocephalus inimicus* nymph parasitized by *Gonatopus erythrodes*; 28, ventral view of *Chlorotettix unicolor* nymph parasitized by *Chelognus* sp.; 29, side view of *Liburnia campestris* adult parasitized by *Haplogonatopus americanus*; 30, dorsal view of *Brucomorpha oculatus* parasitized by *Phorbas mirabilis*.

The sac itself is of various shapes, sizes and colors. Those of *Aphelopus* (Figs. 23, 24 and 25) are elongate oval, and those of *Chelogynus* are rounded and much compressed. Between these two types there are all sorts of gradations. Black is the predominating color and there are variations from it to brown and yellow. Many are green or blue-green, and others are banded transversely with alternate stripes of light and dark brown. In the latter case the colors are arranged segmentally. When the skin that is to form part of the sac is molted it is light colored and not pigmented and modified. As it becomes exposed to the air it assumes the black or fuscous color of the sac. In *Phorbas* the exuvium is pale yellow when first molted, but soon each spiracle is surrounded by a black spot. As previously noted, these enlarge and become confluent, the exuvium finally becoming jet black in color. Invariably the first exuvium is smooth and shining, the second often crinkled or sculptured on its outer margin, and the third is generally very distinctly rugosely sculptured by raised zig-zag lines or is punctate. The sac is located in diverse positions, according to the genus of the parasite. In *Echthrodelpfax*, *Paradryinus*, *Thaumatordryinus* and *Neodryinus* it is found on the thorax beneath the wing. In *Phorbas* (Fig. 26), from various places on the abdomen. In most of the *Anteon* species (Fig. 30), on the ventral side under the hind legs, in *Paranteon* on the abdomen, ventral as well as dorsal, seldom on the sternum or propleura, in *Pseudogonatopus* on the dorsal and lateral sides of the abdomen, in *P. stenocrani* Perk., upright between both wings (Perkins, 1905). In *Gonatopus* (Fig. 27) it is on the side of the abdomen, in *Haplogonatopus* (Fig. 28), on the dorsal posterior part of the abdomen, in *Chelogynus*, (Fig. 29), on the side of the thorax, and in *Aphelopus* on the sides of the abdomen between the first few segments. It always projects between two segments. Often the spiracles of the different exuviae composing the sac can be seen if it is light colored.

Cocoon.—The cocoon is either spun below the ground as is the case with *Aphelopus*, *Chelogynus*, or *Phorbas*, or above on some convenient object, as with *Haplogonatopus*, or some species in *Gonatopus*. That of *Aphelopus*, (Fig. 31), is small, oval, and white, of *Chelogynus*, (Fig. 33), larger, oval, plastered over with sand grains or soil particles, and that of *Bocchus*, (Fig. 32), tough, thick, brown and fibrous, with soil particles

mixed all through it. Many spun above the ground as in some species in *Gonatopus*, (Fig. 34), are white, shining, and very like a spider's cocoon. According to Perkins (1905) the cocoons of *Paradyinus* are often adorned with bits of leaf tissue, that of *Neodryinus* roofed over with the ruptured larval sac which is removed from the hopper and attached. The cocoon of *Prodryinus ormenidis* (Ashm.) is spun beneath the dead hopper (Swezey, 1903). The cocoon is always composed of two parts, and inner more compact structure, within a more loosely woven part.

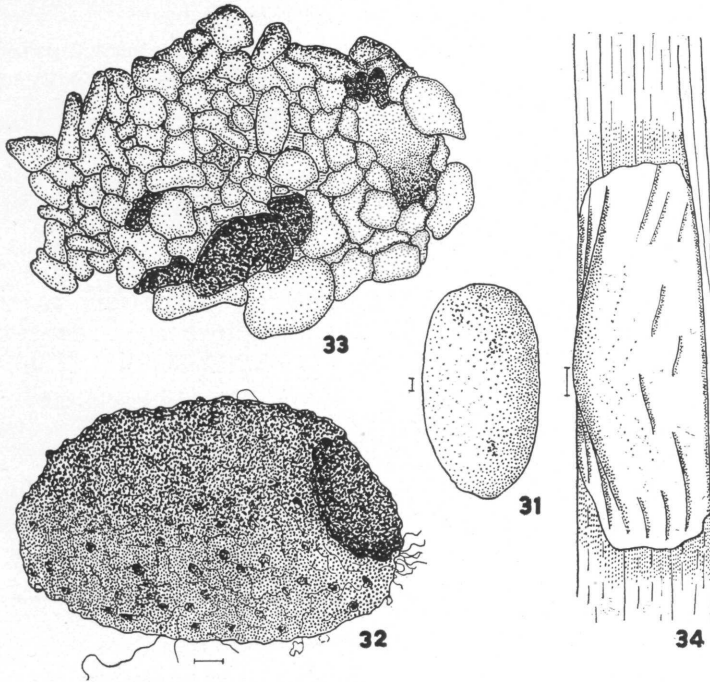


FIGURE 4.

31, cocoon of *Aphelopus* sp., 32, cocoon of *Phorbas mirabilis*; 33, cocoon of *Chelogyne* sp.; 34, cocoon of *Haplogonatopus americanus*.

INTERNAL ANATOMY OF THE LARVA.

Internally the mature larva presents the following characteristics. The mouth leads into a narrow pharynx-esophagus the limits of either of the latter not being definable. This opens into a very large, thick-walled mid-intestine, which is blind at its posterior end, not being connected with the hind-

intestine, which, however, is present at this stage. The pharynx-esophagus is long, extending back to the hind thoracic segment. It is very narrow with a small lumen for the greater part of its length, but broadens out gradually at first, then abruptly, into the mid-intestine. The latter occupies the greater part of the body cavity and becomes greatly distended at maturity, food being taken in much more rapidly than it can be digested, so that the entire mid-intestine acts as a food reservoir.

A set of powerful muscles is attached to the dorsal part of the pharynx-esophagus and a smaller set below it. These act in such a way that their contraction forces this structure open, thus forming a sucking organ. Aside from these the only other striped muscles in the larva of note are those controlling the mandibles. The cells of the pharynx-esophagus are small. Those of the anterior fourth of the mid-intestine are large, columnar, and digestive in function, in contrast to those of the greater part, which are elongate and flattened.

The salivary glands are very large, appearing as two sets of long convoluted tubes, one on each side of the mid-intestine, extending about three-fourths the way down it in the mature larva. Each set is composed of two branches ending anteriorly in a short lateral tube. These two lateral branches open into a common duct which extends into the spinneret. They serve primarily as silk glands in the spinning of the cocoon. The cells composing the main duct are columnar, thus differing distinctly from those of the rest of the glands. Undoubtedly the true salivary function is principally confined to this section of the glands.

There is no caudal vesicle on the larva as observed for *Apanteles* (Tower, 1916), and no malpighian tubes have been observed in any of the stages. Whether the waste products are absorbed and discharged upon pupation, or whether they are thrown off into the host is not known. The ten pairs of spiracles lead into short lateral tracheæ which open into the two longitudinal trunks, the tracheal system in the mature larva being very similar to the general type found. As in the third instar the nervous chain consists of eleven ganglia.